Factors promoting maternal trophic egg provisioning in non-eusocial animals

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Abstract

The adaptive function of trophic egg-laying is generally regarded as extended parental investment to the offspring. However, the evolutionary factors promoting trophic egg-laying are still unclear, because the amount of maternal investment per offspring should be ideally equal between smaller offspring with trophic eggs and larger offspring without any additional investment. Several authors have suggested that trophic egg-laying should evolve only when egg size is constrained, but this hypothesis has not been evaluated. We investigated the evolutionary mechanisms of trophic egg-laying by two different approaches. First, we evaluated morphological constraints on egg size in two sibling ladybird species, *Harmonia axyridis*, which is known to produce trophic eggs, and *H. yedoensis*. Second, we theoretically predicted the optimal proportion of trophic eggs to total eggs and egg size in relation to environmental heterogeneity, predictability of environmental quality, and investment efficiency of trophic egg consumption. The intra- and interspecific morphological comparisons suggest that morphological constraints on the evolutionary determination of egg size are weak at best in the two ladybird species. Moreover, we theoretically showed that small egg size and trophic egg-laying are favoured in heterogeneous environments when mothers cannot adjust egg

size plastically. We also showed that even a small reduction in investment efficiency makes a trophic egg strategy unlikely, despite relatively high environmental predictability. We conclude that trophic egg provisioning may be a flexible maternal adaptation to a highly heterogeneous environment rather than a response to a morphological constraint on egg size.

Keywords Egg size · Environmental heterogeneity · *Harmonia* · Maternal investment · Morphological constraint · Phenotypic plasticity

Introduction

Trophic eggs (also called nurse eggs) are non-developing eggs or egg-like structures produced for offspring consumption (Crespi 1992). Strictly speaking, trophic egg-laying is an evolved maternal phenotype, not simply the unavoidable production of non-developing eggs that happen to be eaten by offspring (Crespi 1992, Perry and Roitberg 2006). Trophic egg-laying occurs in diverse animal taxa with various parental care systems (e.g., non-social and eusocial arthropods, gastropods, amphibians, fishes; reviewed by Perry and Roitberg 2006), although it is often confined to only a few species within a taxonomic group (Elgar and Crespi 1992). In general, the adaptive function of trophic egg-laying is regarded as extended parental investment to the offspring (Alexander 1974, Polis 1984). However, the amount of maternal investment per offspring should be ideally equal between smaller offspring with trophic eggs and larger offspring without any additional parental investment (Baur 1990, Dixon 2000). Therefore, evolutionary factors promoting trophic egg-laying, instead of larger offspring size, are still not understood.

Several studies have suggested that trophic egg-laying should evolve only when egg size is constrained (Alexander 1974, Polis 1984, Mock and Parker 1997, Dixon 2000).

Morphological constraints on egg size such as the size of the ovipositor or pelvic aperture may prevent small females from producing large eggs (Congdon and Gibbons 1987) and thus may lead to the evolution of trophic egg-laying. Moreover, other hypotheses based on the density effect of competing offspring (Parker and Begon 1986) and the physiological constraints (Sakai and Harada 2001) also explain why larger mothers produce larger offspring. In fact, many field studies of diverse animal taxa have documented positive correlations between maternal size and offspring size (Fox and Czesak 2000). However, no studies have evaluated whether mothers that produce trophic eggs exhibit such constraints on maternal body size.

Adaptive mechanisms that might promote trophic egg-laying should be considered in situations where morphological constraints on egg size are not critical. Trophic egg-laying occurs in several groups of eusocial Hymenoptera (Sakagami 1982, Hölldobler and Wilson 1990, Crespi 1992), but it is difficult to examine the adaptive significance of trophic eggs in eusocial systems because complicated conflicts among colony members may obscure the origin and evolution of trophic eggs (Crespi 1992). By contrast, in non-eusocial taxa, the adaptive function of trophic eggs for offspring survival has been examined by focusing on environmental heterogeneity (Kudo and Nakahira 2005, Perry and Roitberg 2005a). In fact, studies have documented that females of some

82 non-eusocial species that face highly heterogeneous environments adopt a trophic egg
83 strategy (e.g., Crump 1981; Kudo and Nakahira 2004). However, maternal fitness
84 between the two strategies, (1) producing small offspring with trophic eggs and (2)
85 producing large offspring without any additional investment, has not been compared
86 explicitly. For such a comparison, a model that can predict which strategy is
87 evolutionarily stable in a heterogeneous environment needs to be developed.
88 Such a model must take into account the unavoidable costs and limitations that are
89 likely to accompany a trophic egg strategy in a heterogeneous environment. As in any
90 strategy involving adaptive phenotypic plasticity (Berrigan and Scheiner 2004, Marshall
91 and Uller 2007), cues that reliably predict future environment conditions must be present
92 for flexible trophic egg provisioning to evolve. However, the environment that the
93 offspring will face is not always predictable, especially in species in which offspring and
94 adult individuals occupy different niches (Werner and Gilliam 1984, Fischer et al. 2011).
95 Although to reduce the level of uncertainty, mothers can collect information that will be
96 useful in making provisioning decisions (Dall et al. 2005), in a variable environment, a
97 certain level of uncertainty is likely to persist. Moreover, even when mothers can collect
98 information accurately, it may be difficult to compensate for environmental quality in
99 through provisioning without specialized morphology and physiology for trophic egg

production, such as distinct ovariole structure and cellular development. Indeed, in the predatory ladybird *Harmonia axyridis* which lacks specialized trophic egg structure (Osawa and Yoshinaga 2009), mothers can manipulate the proportion of trophic eggs depending on the prey availability, but the ratio of trophic to viable eggs is variable even in the highly standardized laboratory conditions (Perry and Roitberg 2005a). As a result, the possibility exists that mothers will provision the 'wrong' amount of resources to their offspring. Furthermore, consumption of trophic eggs is likely to involve some waste of maternal resources (Elgar and Crespi 1992). However, no study incorporating such costs and limitations has thus far examined the conditions that favour the trophic egg-laying.

In this study, we investigated the evolutionary mechanisms that favour trophic egg-laying by making morphological comparisons and by mathematical modelling. First, we compared egg size and maternal body size both intra- and interspecifically in two sibling ladybird species, *Harmonia axyridis* Pallas and *Harmonia yedoensis* Takizawa. Adult body size is quite similar in these two ladybird species (Sasaji 1998), and the hatched larvae of both species eat clusters of sibling eggs, both undeveloped eggs and developing eggs with delayed hatching (Kawai 1978, Osawa 1992a, Osawa and Ohashi 2008). The sibling egg consumption by hatchlings can be regarded as an adaptive maternal phenotype in both *H. axyridis* (Perry and Roitberg 2005a) and *H. yedoensis*

(Noriyuki et al. 2011). If morphological constraints on egg size exist, a positive correlation between egg size and maternal body size would be expected within each species, because smaller mothers cannot produce larger eggs (Fox and Chezak 2000, Fischer et al. 2002, Noriyuki et al. 2010). In addition, if morphological constraints prevent *H. axyridis* females from producing large eggs, then the similar-sized *H. yedoensis* females should not be able to produce eggs larger than those of *H. axyridis*. Furthermore, in females of both species we also examined the ovariole number, which is an important determinant of egg size for a given maternal body size in insects (Gilbert 1990, Stewart et al. 1991a). Thus, we evaluated the role of morphological constraints by comparing and assessing morphological traits in these two sibling ladybird species.

Second, we constructed a mathematical model to predict the optimal proportion of trophic eggs and egg size that mothers should produce. Under spatially and temporally heterogeneous environments for offspring survival, we investigated how reliable the environmental cues available to the mother have to be for a trophic egg strategy to be favoured by selection. Additionally, we incorporated the fact that a certain proportion of maternal resources provided as trophic eggs are not consumed by the offspring and examined whether natural selection favours trophic egg-laying despite its cost. Finally, on the basis of the results of these different two approaches and the findings of previous

136 studies, we propose a reasonable explanation for the widespread occurrence of trophic
137 egg-laying in non-eusocial animals.
138
139 **Methods**
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141 Morphological measurements
142
143 The generalist predator *H. axyridis* and the specialist predator *H. yedoensis* are sibling
144 species with sympatric distributions in central Japan (Noriyuki et al. 2011). Females of
145 the two species produce undeveloped eggs which are consumed by the sibling hatchlings
146 (Osawa and Ohashi 2008). However, the precise developmental mechanisms regulating
147 the production of undeveloped eggs are not fully understood. Indeed, it is possible that
148 gamete incompatibility and sperm limitation cause the failure of fertilization (e.g., Wedell
149 et al. 2002). Moreover, eggs can be infected by male-killing bacteria and killed male
150 embryos appear as infertile eggs in both *H. axyridis* (Majerus et al. 1998) and *H.*
151 *yedoensis* (N. Osawa, unpublished data), although uninfected females also produce
152 certain proportion of undeveloped eggs. The absence of micropyles is one criterion used
153 to categorize an egg as trophic in the Hymenotera and Heteroptera (e.g., Gobin et al. 1998,

154 Kudo et al. 2006), but in *H. axyridis*, micropyles are present in the shells of both
155 developing and undeveloped eggs (Osawa and Yoshinaga 2009). In addition, there is no
156 special feature of the spatial distribution of undeveloped eggs within the clutch in *H.*
157 *axyridis* (Perry and Roitberg 2005a). However, the proportion of undeveloped eggs
158 increases when *H. axyridis* mothers face the low resource availability (Perry and Roitberg
159 2005a) and consumption of undeveloped eggs enhance the survival of hatchlings
160 especially when aphid density is low (Osawa 1992a), in a manner consistent with a
161 definition of adaptive trophic egg provisioning (Perry and Roitberg 2006). Although *H.*
162 *yedoensis* mothers have not been definitely proved to produce trophic eggs in the strict
163 sense (cf. Perry and Roitberg 2006), the consumption of undeveloped eggs greatly
164 enhances prey capture performance in *H. yedoensis* hatchlings, suggesting that the
165 production of undeveloped eggs has evolved as an adaptive maternal phenotype
166 (Noriyuki et al. 2011). Therefore, even though precise proximate mechanisms have not
167 been identified, the production of undeveloped eggs in *H. axyridis* and *H. yedoensis* can
168 be regarded as an adaptive maternal strategy for the offspring survival.

169 We collected 10 *H. axyridis* adults at the Botanical Garden of Kyoto University,
170 Kyoto (135°47’E, 35°02’N), and 25 egg clusters of *H. yedoensis* at Hieidaira, Shiga
171 (135°83’E, 35°02’N), in May 2008. We obtained eggs from the adults and the egg

clusters, and reared the resulting offspring at each stage in plastic cups (13 cm wide, 10 cm high) to the adult stage at 25 ºC, 16L:8D, and about 70% relative humidity. We provided the larvae with a surplus of frozen *Ephestia kuehniella* Zeller eggs (Beneficial Insectary, Inc., Redding, California, USA). We randomly chose 54 newly-emerged and unmated individuals (27 females and 27 males) of *H. axyridis* and 48 newly-emerged and unmated individuals (24 females and 24 males) of *H. yedoensis* from the stock for the experiment. We used first-generation offspring because (1) there were not enough adults of *H. yedoensis* in the original field collection for a valid statistical analysis, and (2) it allowed us to use larval morphology to confirm the identities of the two species, which are almost impossible to distinguish on the basis of adult morphology (Sasaji 1998).

To obtain eggs from the first-generation adults, we reared mated females individually with a surplus of frozen eggs at 25 ºC, 16L:8D, and about 70% relative humidity. We used 10 eggs from each of five different clutches laid by each female for data analysis, except if the number of eggs in a clutch was less than 10, then all eggs in that clutch were measured. In the case of a female that laid fewer than five clutches, we measured 10 eggs from each clutch that she laid. We measured both egg height (h) and width (r) under a stereo microscope (Carl Zeiss® SV-11 APO) to the nearest 0.025 mm. We estimated egg size as the egg volume calculated using the formula $hr^2\pi/6$ (mm^3;

Takakura 2004). We measured body length with a slide calipers to the nearest 0.01 mm and used as maternal body size. After a female died or had laid five clutches, we examined her number of ovarioles under the stereo microscope.

Statistical analysis

We took into account the fact that the sizes of eggs from the same clutch or laid by the same mothers are not statistically independent. To test for a correlation between maternal body size and egg size, we adopted a regression model with more than one value of the dependent variable (egg size) per value of the independent variable (maternal body size; Sokal & Rohlf 1995). We used nested analysis of variance (nested ANOVA) with mothers within ladybird species, and with clutches within mothers, to compare egg size between ladybird species. We analyzed the effects of maternal body size and ladybird species on ovariole number by analysis of covariance (ANCOVA). All statistical analyses were carried out with JMP® 7 (SAS Institute Japan).

The model

We present the simplest theoretical framework for the evolution of trophic egg-laying that incorporates environmental heterogeneity, environmental predictability, and investment efficiency of trophic eggs. We assume that mothers cannot adjust egg size plastically. This assumption is applicable to many kinds of animals because ovariole or pelvic aperture size should remain unchanged in a given individual female. In fact, egg size appears to be inflexible within individual females in many animals, such as land snails (Baur 1988, Baur and Raboud 1988), insects (Stewart et al. 1991a, 1991b, Dixon and Guo 1993, Soares et al. 2001), and birds (Christians 2002), and this inflexibility may be tied to ovariole or pelvic aperture size. Even though some species are able to manipulate egg size in response to the quality of the oviposition site (Leather and Burnand 1987, Fox et al. 1997, Mizumoto and Nakasuji 2007), plastic adjustment of egg size is uncommon in animal taxa and the degree of the egg size variation seems to be highly constrained (e.g., Kawecki 1995). In addition to morphological factors, physiological mechanisms of oogenesis may also constrain the immediate adjustment of egg size. Therefore, we assume instead that egg size can evolve to an optimal value and that mothers can produce trophic eggs to deal with an adverse environment. We assume that trophic eggs and viable eggs are the same size, because no general size difference trend has been reported. Moreover, we assume that trophic and viable eggs provide equal food quality for

offspring survival, although possible differences in chemical composition and function between these eggs have not been examined. For simplicity, we assume that the total amount of maternal resources that can be allocated to the offspring as viable eggs and trophic eggs is the same for all females and fixed to 1.

To model the simplest possible variable environment, we examine an environment with only two states: good and poor. The relationship between investment per offspring and offspring fitness differs between the two environments because of biotic or abiotic factors. Moreover, we do not distinguish between spatial and temporal variation. We specify that the minimum viable offspring size is smaller in the good environment than in the poor environment, because an offspring should require fewer resources to become established in the more favourable environment (Fox et al. 1997). We also assume that, for offspring of a given size, offspring fitness is greater in the good environment than in the poor environment (McGinley et al. 1987). Furthermore, we assume that low levels of maternal investment result in zero fitness for offspring because they need a threshold amount of resource to survive, and that fitness approaches an asymptote at high levels of parental investment because offspring cannot make full use of excess resources (Smith and Fretwell 1974, Parker et al. 2002). Thus, we describe the relationship between offspring fitness S and viable egg size in the good environment by $S_{\mathrm{G}}(e)=1-(1/e)^2$ and

244 in the poor environment by $S_P(e)=1-(k/e)^2$, where the subscripts G and P indicate the
245 good and the poor environment, respectively, *e* is viable egg size and trophic egg size, and
246 *k* is a constant that specifies the difference in quality between the two environments. To
247 make the labels 'good' and 'poor' biologically feasible, we assume $k > 1$ such that
248 offspring survive better in a good environment. We assume that individual females
249 experience the two habitat types, good and poor, in the proportion *p* and $1 - p$,
250 respectively.

251 We define environmental predictability, *q*, as the probability that maternal
252 assessment of the environmental quality is correct. Specifically, we assume that when
253 mothers incorrectly assess a poor environment as a good environment, then they do not
254 provision trophic eggs although the offspring may need them to survive. Conversely,
255 when maternal assessment of the good environment is wrong, then mothers may
256 provision unneeded trophic eggs, causing per offspring maternal investment to exceed the
257 optimal value (Table 1). For simplicity, we assume that predictability *q* is constant across
258 environmental situations. If $q = 1$, then mothers can assess the environmental quality
259 perfectly and provision the optimal proportion of trophic eggs in each environment; in
260 contrast, if $q = 0.5$, then mothers provision trophic eggs with a probability of 0.5
261 irrespective of the environmental quality. Because $q < 0.5$ is not realistic, we consider

only situations with $0.5 \le q \le 1$ in the analysis.

From the above assumptions it follows that the ratio of trophic eggs to the total amount of maternal investment is given by $p(1-q)t + (1-p)qt = t(p+q-2pq)$, where t is the ratio of trophic eggs to the amount of maternal investment when maternal assessment is wrong in the good environment or correct in the poor environment (that is, the amount of resource when mothers 'evaluate' the environment as poor; Table 1). Similarly, the number of viable eggs in an environment that mothers evaluate as poor is given by $\{p(1-q)(1-t) + (1-p)q(1-t)\}/e = \{(1-t)(p+q-2pq)\}/e$. Hence, per offspring maternal investment in an environment that mothers evaluate as poor is given by $e + t(p+q-2pq)\delta \div \{(1-t)(p+q-2pq)\}/e = \{1+\delta t/(1-t)\}e$, where δ is the investment efficiency of trophic egg consumption, defined as the proportion of the trophic egg amount consumed by the offspring. Because the total amount of maternal investment is fixed to 1, the amount of maternal investment that is provided as viable eggs in both environments is given by $1-t(p+q-2pq)$. Therefore, maternal fitness can be described as the product of offspring number times the probability of offspring survival in each environment:

$$W(e,t) = \frac{1-t(p+q-2pq)}{e}\left\{p\left(qS_{\mathrm{G}}[e] + (1-q)S_{\mathrm{G}}\left[\left(1+\frac{\delta t}{1-t}\right)e\right]\right) + (1-p)\left(qS_{\mathrm{P}}\left[\left(1+\frac{\delta t}{1-t}\right)e\right] + (1-q)S_{\mathrm{P}}[e]\right)\right\}$$

Results

280

281 Morphological comparisons

282

283 Mean female body length was not significantly different between *H. axyridis* (mean ± SE
284 = 7.03 ± 0.09 mm, n = 27) and *H. yedoensis* (7.24 ± 0.10 mm, n = 24; Student's t test, t_{49}
285 = –1.67, P = 0.10). Female body length and egg volume were not significantly related in
286 either species (linear regression analysis, *H. axyridis*: $F_{1, 25}$ = 0.16, P = 0.69, r^2 = 0.003; *H.*
287 *yedoensis*: $F_{1, 22}$ = 0.25, P = 0.62, r^2 = 0.005; Fig. 1). Mean egg volume was significantly
288 smaller in *H. axyridis* (mean ± SE = 0.2478 ± 0.0011 mm^3, n = 1150) than in *H. yedoensis*
289 (0.3481 ± 0.0013 mm^3, n = 1046; nested ANOVA, $F_{1, 49}$ = 5458.62, P < 0.0001; female
290 code [species]: df = 49, F = 53.9136, P < 0.0001; clutch code [female code]: df = 187, F =
291 6.3250, P < 0.0001). There were significant maternal body size and species effects on
292 ovariole number but no maternal body size × species interaction was detected (ANCOVA,
293 maternal body size: $F_{1, 47}$ = 9.09, P < 0.01; species: $F_{1, 47}$ = 96.10, P < 0.0001; interaction:
294 $F_{1, 47}$ = 1.63, P = 0.21; Fig. 2).

295

296 Model analysis

297

We present our results as graphical solutions owing to the complexity of the model. We first consider the special case in which the maternal resource in the trophic eggs is completely consumed by the offspring (i.e., $\delta = 1$). The effects of the proportion of the good environment (p) on the optimal proportion of trophic eggs and on egg size are depicted graphically in Fig. 3. The optimal proportion of trophic eggs relative to p is a convex upward curve (Fig. 3a), and the optimal egg size decreases with p (Fig. 3b).

The effects of environmental predictability (q) on the optimal proportion of trophic eggs and on egg size are depicted graphically in Fig. 4. The optimal proportion of trophic eggs is always zero when it is not possible to predict the environment ($q = 0.5$), and it increases as predictability increases (Fig. 4a).

The effects of the magnitude of the difference in quality between the good and poor environments (k) on the optimal proportion of trophic eggs and on egg size are depicted in Fig. 5. Both the proportion of trophic eggs and egg size increase with k, but the rate of increase in the proportion of trophic eggs decays as k increases (Fig. 5a), whereas optimal egg size increases linearly with k (Fig. 5b).

Finally, we consider the case that the trophic egg resource is not completely consumed by the offspring ($0 \leq \delta \leq 1$). Despite the costs associated with trophic egg consumption, a trophic egg strategy can evolve in heterogeneous environments (Fig. 6a).

316 In fact, the greater the difference in quality between two environments, the larger the area
317 in the parameter space where a trophic egg strategy is favoured ('trophic egg area', grey
318 and black in Fig. 6). However, trophic egg area severely decreases as investment
319 efficiency decrease, especially when the difference in quality between two environments
320 is small (k = 1.5, Fig. 6b).
321
322 **Discussion**
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324 Here we present three key findings in trophic egg evolution. First, intra- and interspecific
325 morphological comparisons suggest that maternal body size is at best a weak
326 morphological constraint on egg size in *H. axyridis*, which has been experimentally
327 proved to produce trophic eggs (Perry and Roitberg 2005a), and *H. yedoensis* (Fig. 1).
328 Second, we find that trophic egg-laying is expected to evolve in heterogeneous
329 environments when mothers cannot manipulate egg size plastically (Fig. 3a). Third, we
330 theoretically show that a small reduction in investment efficiency in tropic egg
331 consumption greatly reduces the likelihood of trophic egg evolution, even when cue
332 reliability is relatively high (Fig. 6). Taken together, these finding lead us to conclude that
333 maternal adaptation to highly heterogeneous environments rather than morphological

334 constraints on egg size is a sufficient explanation for the evolution of trophic egg-laying
335 in some non-eusocial animals.

336 This is the first study to evaluate the role of morphological constraints on egg size in
337 species that produce trophic eggs. We found no significant correlation between egg size
338 and maternal body size in *H. axyridis* or *H. yedoensis* (Fig. 1), indicating that smaller
339 females can produce eggs similar in size to the eggs of larger females. Moreover, the
340 relationship between egg size and maternal body size was extremely weak in both species,
341 accounting for less than 1% of the total variation in egg size. Furthermore, *H. yedoensis*
342 females produce larger eggs than *H. axyridis* females, despite the similar maternal body
343 size in the two species (Fig. 1). A reduction in the number of ovarioles should contribute
344 to the production of larger eggs relative to maternal body size (Fig. 2). This result is
345 consistent with the previous finding that species of ladybirds with few ovarioles lay larger
346 eggs than similar-sized species with many ovarioles (Stewart et al. 1991a). These results
347 suggest that maternal body size as a morphological constraint has at best a minor role in
348 the determination of egg size in the two studied ladybird species. Recent studies of insects
349 also suggest that the importance of morphological constraints on the evolution of egg size
350 has been overemphasized (Fischer et al. 2002, Bauerfeind and Fischer 2008, Noriyuki et
351 al. 2010). Importantly, morphological constraints are particularly unlikely to exist when

352 eggs are small relative to the size of the mother, as is the case in most insect species as
353 well as tree frogs and sharks that produce large numbers of trophic eggs. In addition, even
354 if morphological constraints prevent small females from producing eggs of optimal size,
355 such females can overcome such constraints by producing more elongated eggs
356 (Congdon and Gibbons 1987). In the subsocial bug *Adomerus triguttulus*, viable eggs are
357 more elongated than trophic eggs (Kudo et al. 2006), suggesting that the females may
358 have potential to overcome morphological constraints on egg size by changing the egg
359 morphology. Moreover, in several reptiles, smaller mothers produce elongated eggs,
360 presumably to facilitate their smooth passage out of the mother's body (Sinervo and Licht
361 1991, Clark et al. 2001, Ji et al. 2006, Rollinson and Brooks 2008). Therefore, it is
362 possible that morphological constraints may not adequately account for trophic egg
363 evolution in other animals.

364 Instead, our theoretical model showed that trophic egg provisioning to small
365 offspring is favoured in heterogeneous environments when mothers cannot manipulate
366 egg size plastically (Fig. 3). Optimal per offspring maternal investment in a poor
367 environment can also be achieved by the evolution of large eggs, without trophic
368 egg-laying, because very large offspring can survive despite variation in environmental
369 quality. As a result, in some circumstances selection favours females that consistently

produce large eggs. Females following this non-plastic strategy, however, are obligated to invest an amount of resources in excess of the optimal value in the good environment, which does not require a large amount of maternal resources. In contrast, by following a trophic egg-laying strategy, females can change their per offspring maternal investment even after deposition of viable eggs, suggesting that trophic egg production and consumption by hatchlings allows females to flexibly adapt to a variable resource environment.

Note that the maximum proportion of trophic eggs is predicted when $0.5 < p < 1$ (Fig. 3a). This result indicates that trophic egg-laying tends to be favoured when the proportion of the good environment is higher than the proportion of the poor environment. This result may appear counterintuitive, because we assume that mothers provision trophic eggs to deal with a poor environment. However, although the large egg strategy is inflexible, it can consistently achieve a high offspring survival rate even in a poor environment. By contrast, a trophic egg strategy may lead to large reductions of fitness and offspring survival in a poor environment if the mother incorrectly assesses the environmental quality and therefore fails to provide trophic eggs to small offspring. Thus, a large egg strategy, which should be a safe strategy even in a poor environment, may be favoured when the proportion of poor environment is relatively high.

388 Our conclusion that evolution of trophic eggs requires a highly heterogeneous
389 environment is consistent with the empirical reports in both vertebrates and invertebrates
390 (e.g., Crump 1981, Dixon 1998). For example, in aphidophagous lacewings and ladybirds,
391 food resources are frequently and intermittently limited over time because of the
392 ephemeral nature of aphid colonies (Osawa 1992b, Hemptinne et al. 1992, Dixon 1998),
393 and they are also spatially heterogeneous in quality and quantity (Osawa 2000). In
394 sub-social animals that provide parental care to offspring even after the hatching (e.g.,
395 tree frogs, burrower bugs, and passalid beetles), as well as predatory animals without
396 effective natural enemies (e.g., sharks and ladybirds), mothers may have relatively long
397 ecological longevity and thus may experience various environmental conditions over
398 their reproductive period. Therefore, it is suggested that trophic egg provisioning may
399 function as a flexible solution for dealing with multiple habitats (Perry and Roitberg
400 2006). Because in our model we do not distinguish between spatial and temporal
401 variation, our findings are potentially applicable to diverse animal taxa producing trophic
402 eggs to cope with predictable environmental variation.

403 Our model revealed that environmental predictability enhances the likelihood that
404 trophic egg provisioning to small eggs will evolve (Fig. 4). Our result indicates that the
405 evolution of trophic egg-laying is possible in heterogeneous environments if mothers

406 have even a little ability to estimate the offspring's environment ($q \geq 0.5$). However, recall
407 that this result holds only when the investment efficiency of trophic egg consumption δ is
408 1 (results with $0 \leq \delta \leq 1$ are discussed below).

409 In some species with trophic egg-laying, mothers are known to evaluate
410 environment conditions that their offspring will face in several ways. For example, in tree
411 frogs, mothers adjust the number of trophic eggs based on the number of offspring (Kam
412 et al. 1998) and offspring age (Gibson and Buley 2004). In *A. triguttulus* females adjust
413 the number of trophic eggs per viable egg in response to varying resource environments
414 prior to oviposition (Kudo and Nakahira 2005). However, in a majority of trophic egg
415 laying species, the role of environmental cues in trophic egg provisioning has not been
416 examined (Perry and Roitberg 2006). In order to evaluate our model prediction that
417 environmental predictability should be necessary for evolution of trophic egg-laying (Fig.
418 4), empirical tests are required to detect maternal plasticity in trophic egg-laying.

419 Our model also demonstrated that the evolution of trophic eggs is highly sensitive to
420 the wasteful expenditure of maternal resource for trophic eggs even when environmental
421 predictability is relatively high (Fig. 6). In particular, when environmental quality does
422 not differ very much between the good and poor environments (k = 1.5 in Fig. 6), even a
423 small reduction of investment efficiency makes the evolution of trophic egg-laying

424 unlikely. Both nutritive parts of trophic eggs and the shells may be left uneaten by
425 offspring (Perry and Roitberg 2005a). Moreover, non-sibling conspecific individuals and
426 other predators attack trophic eggs, especially in species with no post-natal parental care
427 but also in sub-social animals (Osawa 1989, Nomakuchi et al. 2001). We suggest
428 therefore that these moderate but unavoidable costs associated with trophic egg
429 consumption may mitigate against the evolution of trophic egg-laying, thus accounting
430 for the evolution of trophic egg laying in some taxa and not others.

431 Variation in the division of maternal resources among siblings may impose both
432 costs and benefits on maternal trophic egg provisioning, although our model does not
433 explicitly consider this mechanism. Classical optimal investment theory predicts that the
434 amount of parental resource per offspring should be constant in a given environment
435 (Smith and Fretwell 1974). In real organisms, however, the amount of parental resource
436 per offspring in a brood with trophic eggs frequently varies among siblings (Osawa
437 1992a), because hatching asynchrony and trophic egg location in the clutch, for example,
438 may cause a bias in resource allocation (Osawa 1992a, Perry and Roitberg 2005a).
439 Moreover, adults that abandon their eggs presumably have little ability to control the
440 distribution of resources among offspring. Thus, it is suggested that biases in resource
441 allocation among siblings may prevent mothers from producing trophic eggs. Conversely,

442 trophic egg-laying may operate as a bet-hedging strategy by generating variation in the
443 size of offspring, the largest of which can survive in the event of unpredictable poor food
444 availability (Perry and Roitberg 2006). In support of this argument, some empirical and
445 comparative studies suggest that within-clutch variation in egg size can reflect an
446 adaptive strategy for dealing with in unpredictable environments in diverse animal taxa
447 such as frogs and fishes (Crump 1981, Einum and Fleming 2004, Marshall et al. 2008,
448 Crean and Marshall 2009). However, the bet-hedging hypothesis for trophic eggs has yet
449 to be tested against the alternative hypothesis of a single optimum in provisioning per
450 offspring. Further investigation of bet-hedging as an evolutionary mechanism promoting
451 trophic egg provisioning should be a productive area of investigation.

452 Our model results are consistent with the findings of previous theoretical studies on
453 adaptive phenotypic plasticity (Berrigan and Scheiner 2004). Specifically, models of
454 phenotypic plasticity generally show that plasticity is favoured when (1) there is
455 environmental heterogeneity (spatial or temporal), (2) there are cues that reliably predict
456 future environmental conditions, and (3) the cost of plasticity is low. Therefore, we
457 suggest that trophic egg provisioning can be regarded as one strategy of adaptive
458 phenotypic plasticity when plastic adjustment of egg size is constrained.

459 In our model, parental-offspring conflict is not taken into account: We assumed that

offspring cannot influence parental behaviour. Importantly, selection typically maximizes maternal rather than offspring fitness, particularly in species with no post-natal parental care, in which offspring counter-strategies may be less likely to evolve (Smith and Fretwell 1974, Trivers 1974). However, parental-offspring conflict affects the evolution of maternal reproductive strategies if offspring can counteract maternal strategies (Parker et al. 2002, Perry and Roitberg 2005b). In particular, Crespi (1992) discussed hypothetically the evolution of trophic eggs in the context of reduction of parent-offspring conflict over sibling cannibalism. Specifically, he suggests that when parent and offspring interests conflict over sibling cannibalism, mothers might adopt a strategy to limit cannibalism by producing trophic eggs, which are less costly than viable eggs but which provide enough energy to cause offspring to refrain from eating viable siblings (Crespi 1992). This hypothesis and our predictions concerning environmental heterogeneity are not necessarily mutually exclusive. Models that incorporate the offspring's point of view need to be developed to predict whether Crespi’s (1992) argument can function as a general explanation for trophic egg evolution. However, some empirical data refute the generality of the parent-offspring conflict reduction hypothesis. In particular, Kudo and Nakahira (2004) explicitly rejected the hypothesis by showing in careful experiments in the sub-social burrower bug that the presence or absence of trophic

eggs did not affect the rate of sibling cannibalism. Moreover, a cost difference between trophic and viable egg production may not be common in animal species (Perry and Roitberg 2006). Nevertheless, further studies are needed to identify possible differences in quality between trophic and viable eggs to evaluate the parent-offspring conflict reduction hypothesis.

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720 ## Figure legends

721

722 **Fig. 1.** Relationship between female body size and egg size (mean ± SE) by species.

723 Mean volumes of egg produced by *H. axyridis* (open circles) and *H. yedoensis* (closed

724 circles) females of a given body length.

725

726 **Fig. 2.** Relationship between female body size and number of ovarioles in *H. axyridis*

727 (open circles) and *H. yedoensis* (closed circles). Dotted and solid lines represent the linear

728 regression for *H. axyridis* and *H. yedoensis*, respectively.

729

730 **Fig. 3.** Optimal proportion of trophic eggs (a) and optimal offspring size (b) as a function

731 of the proportion of the good environment. Parameter values used are $k = 2.0$, $q = 0.75$

732 (solid line); $k = 4.0$, $q = 0.75$ (dashed line); and $k = 2.0$, $q = 0.90$ (dotted line); where k is

733 the degree of difference between the two environments and q is environmental

734 predictability.

735

736 **Fig. 4.** Optimal proportion of trophic eggs (a) and optimal offspring size (b) as a function

737 of environmental predictability. We did not evaluate the situation where $q < 0.5$ because it

738 is biologically unrealistic. Parameter values used are $k = 2.0$, $p = 0.50$ (solid line); $k = 4.0$,

739 $p = 0.50$ (dashed line); and $k = 2.0$, $p = 0.25$ (dotted line); where k is the difference

740 between the two environments and p is the proportion of the good environment.

741

742 **Fig. 5.** Optimal proportion of trophic eggs (a) and optimal offspring size (b) as a function

743 of the difference in quality between the good and bad environments. Parameter values

744 used are $p = 0.5$, $q = 0.66$ (solid line); $p = 0.25$, $q = 0.66$ (dashed line); and $p = 0.5$, $q =$

745 0.75 (dotted line); where p is the proportion of the good environment and q is

746 environmental predictability.

747

748 **Fig. 6.** Conditions that favour a trophic egg strategy ($t > 0$) when $k = 1.5$ (black area) or k

749 = 2.0 (black and grey areas), depending on the investment efficiency δ (horizontal axis):

750 (a) proportion of good environment p (vertical axis), and (b) environmental predictability

751 q (vertical axis). Other parameters: (a) $q = 0.75$, (b) $p = 0.25$. In the shaded parameter area,

752 a trophic egg-laying strategy is expected to never evolve.

1 # Table

Table 1. Relationship between environmental conditions and maternal investment

Environmental quality	Environmental predictability	Maternal strategy	Per offspring maternal investment*
Good (p)	Correct (q)	Viable eggs only	e
	Wrong ($1 - q$)	Trophic egg provisioning (if necessary)	$\{1 + \delta t/(1 - t)\}e$
Poor ($1 - p$)	Correct (q)	Trophic egg provisioning (if necessary)	$\{1 + \delta t/(1 - t)\}e$
	Wrong ($1 - q$)	Viable eggs only	e

*Model parameters e, t, and δ describe the size of viable eggs, the proportion of trophic eggs, and the investment efficiency of trophic eggs, respectively (see text for details).

2